

Modelling Food Webs

B. Drossel¹ and A. J. McKane^{2,3}

¹Institut für Festkörperphysik, TU Darmstadt, Hochschulstr. 6
D-64289 Darmstadt, Germany

²Departments of Physics and Biology, University of Virginia
Charlottesville, VA 22904, USA

³Department of Theoretical Physics, University of Manchester
Manchester M13 9PL, UK

Abstract

We review theoretical approaches to the understanding of food webs. After an overview of the available food web data, we discuss three different classes of models. The first class comprise static models, which assign links between species according to some simple rule. The second class are dynamical models, which include the population dynamics of several interacting species. We focus on the question of the stability of such webs. The third class are species assembly models and evolutionary models, which build webs starting from a few species by adding new species through a process of “invasion” (assembly models) or “speciation” (evolutionary models). Evolutionary models are found to be capable of building large stable webs.

1 Introduction

Ecological systems are extremely complex networks, consisting of many biological species that interact in many different ways, such as mutualism, competition, parasitism and predator-prey relationships. They have been built up over long, evolutionary time scales, and in some cases will contain extremely ancient structures which hold information on the nature of the evolutionary changes which occurred in the distant past. Understanding and modelling such complex networks is one of the major challenges in present-day natural sciences.

Much research focuses on only a small number of species and their interactions, such as hosts and their parasites, or the relationship of a particular species with its prey or predators. Another important direction of research consists in studying larger networks of species by concentrating on their feeding relationships and on competition between predators, neglecting other types of interaction. Such networks, called food webs, are the subject of this review article. We will only be concerned with community food webs, which describe these interactions between species in a particular habitat, and will not discuss sink webs (species identified when tracing interactions down from a particular chosen species) or source webs

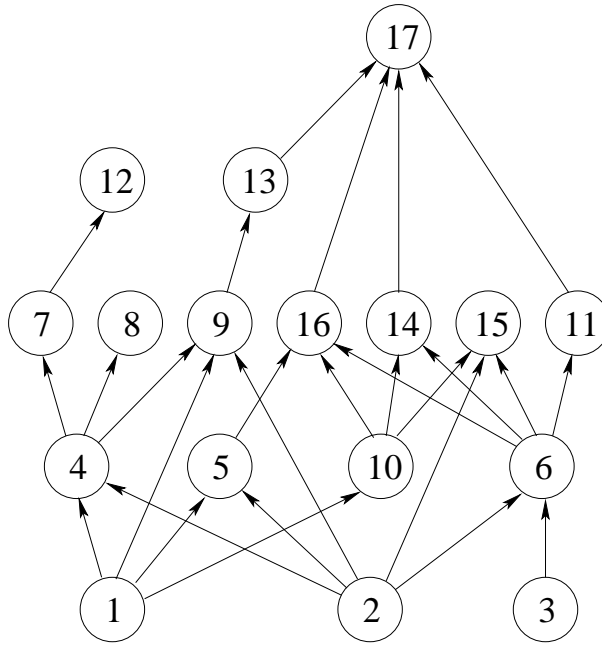


Figure 1: Narragansett Bay food web. 1=flagellates, diatoms; 2=particulate detritus; 3=macroalgae, eelgrass; 4=*Acartia*, other copepods; 5=sponges, clams; 6=benthic macrofauna; 7=ctenophores; 8=meroplankton, fish larvae; 9=pacific menhaden; 10=bivalves; 11=crabs, lobsters; 12=butterfish; 13=striped bass, bluefish, mackerel; 14=demersal species; 15=starfish; 16=flounder; 17=man. (After Kremer and Nixon 1978. *A coastal marine ecosystem*, Springer-Verlag, Berlin.)

(species identified when tracing interactions up from a particular chosen species). From now on community food webs will simply be referred to as food webs, or webs.

The early studies of the natural history of a given habitat were descriptive. It was not until the third quarter of the nineteenth century that the idea of listing the basic information on “what eats what” in a particular habitat, and presenting it in the form of a matrix was born. The usual format has the rows representing predators and the columns representing prey. The matrix elements might be numbers which specify the amount of food consumed, or, since such detail is very rarely known, simply 0’s and 1’s specifying the presence or absence of a predator-prey link. The diagrammatic representation of food webs was introduced some time later (see Fig. 1 for an example). They consist of vertices representing species in the food web, with a directed link — that is a line with an arrow attached — from vertex A to vertex B , if species A is eaten by species B . Notice that the direction of the arrows signifies the flow of resources. These networks illustrate the bare bones of the predator-prey relationships between the species: they miss much of the fine detail such as temporal variations in diet (daily or seasonal), but allow the longer term picture of predator-prey relationships to emerge. Community food webs cannot include all species in a habitat (such

as all the bacteria living within plants and animals), but rather focus on a set of different types of species, which are chosen prior to analyzing their predator-prey relationships. This reduction of the rich, distinctive and complex nature of individual ecosystems tends to be less enthusiastically embraced by field ecologists, than by theoretical ecologists. For many of those in the field, the attraction of the study of natural communities is in their details and unique features. In fact, even when food webs were published by early investigators, they frequently seemed designed to illustrate their complexity, rather than to encourage the theoretical understanding of their form. It was probably this idea of the distinctiveness and natural complexity of food webs that ensured that few theoretical investigations were carried out during the century after the first food webs were constructed.

The change in emphasis in the study of food webs dates from the late 1970's and early 1980's, when many of the published webs were collected together and various regularities were noticed for the first time. During roughly the same period simple models of food webs were formulated. The first models were dynamic, using simple population dynamics, but without incorporating the evolved nature of the web. Static models were also introduced in which species were simply represented as vertices in a graph and directed links between them were drawn according to some rule. The structure of the resulting webs could then be compared to that of real food webs.

Obtaining data on dynamic properties is much more difficult than the already hard task of collecting information on static webs. In any case, many of the time scales of interest to us will be so long as to be inaccessible by direct methods. One aspect which is in some sense intermediate between the static and dynamic descriptions, and which has attracted a large amount of attention, is the question of the stability of food webs. This is frequently couched in terms of the complexity of the food web (here meaning a larger web or one with greater connectance). In other words: does stability increase with web complexity?

To ecologists working in the 1950's and 1960's the answer was clearly "yes". They pointed to the susceptibility of certain cultivated, or other species poor, communities to large scale invasions by pests, and the relative rarity of such outbreaks in naturally rich ecosystems as evidence [1, 2]. Theoretically it was noted that increases in species number or connectance led rapidly to increases in the available number of food chains or pathways in food webs. It then seemed quite compelling to argue that the disruption or elimination of only a few of these pathways, if they were numerous, was not likely to lead to a complete collapse of the web [3].

This consensus was disrupted in the early 1970's by investigations into the linear stability of model ecosystems having random interactions [4]-[6]. They showed that these model ecosystems became less stable as species number or connectivity increased. There are two obvious objections to these conclusions. Firstly, real food webs are not random; they are highly evolved structures. Secondly, the criterion of linear stability analysis as applied to population dynamics equations may not be particularly relevant to real ecosystems, not least because they may not be sufficiently close to equilibrium for a local condition such as this to apply.

Over the next few years both objections relating to the validity of the randomness assumption and to the use of linear stability analysis for real webs, were addressed. Dynamical models with Lotka-Volterra type or more complicated population dynamics were introduced, and the stability and dynamical properties of small networks consisting of a few species were investigated, demonstrating a variety of instances where more complex model systems were not less stable than simpler ones. Furthermore, models were introduced that built up a community by a sequence of invasions or speciations. The most recent of these models lead to the formation of large stable webs, thus demonstrating explicitly that large complex networks can be stable.

The different types of models mentioned above will be reviewed in the following sections, with an emphasis on more recent work. The earlier phase of theoretical work has been well documented in a number of books and articles [7]-[9]. Before concentrating on theoretical developments, however, we will begin (in section 2) by introducing the basic concepts used to describe food webs by reference to real webs, and also briefly allude to the problems in collecting data to construct real webs. In section 3, we will briefly discuss static food web models. Section 4 describes the various types of dynamical models and their contribution to the complexity-stability debate. In section 5, we give an overview of models that build food webs by a sequence of species invasions or speciations. We include simple toy models as well as species assembly models and more sophisticated evolutionary models. Section 6 concludes the article with a brief overview and a look to the future.

2 Basic properties of food webs

In this section we will characterize food webs by introducing the basic features associated with them, quantifying them as much as possible. This will allow comparison between real webs and model webs. As the concepts are defined, we will also briefly discuss additional aspects such as various assumptions made in the definitions, problems or ambiguities associated with the definitions, typical values found in real webs or difficulties in obtaining accurate measurements in the field.

The most primitive concept is the size of the food web, defined by the number of species in the web, S . In published versions of real webs (see, for instance, [9]), the terms “species” may refer to “trophic species”, which is a collective term for all the species having a common set of predators and prey. For this reason general terms such as “ants” or “algae” appear; conversely the same species at different stages in its life-cycle may belong to a different trophic species. The existence of terms such as “detritus” or “dead organic material” in many webs, is also an illustration of the difficulty in deciding what to include and what to omit from the web. Many earlier studies were not very extensive, and frequently the published webs were rather small. For example, the 113 webs listed by Cohen *et al* in their 1990 review [9] vary in size from 5 to 48, with a mean of 17. Since 1990 larger webs have been reported, with several containing more than 100 species [10]-[13].

The next most important quantity associated with a food web is a measure of the number of the interactions between the species. This is frequently taken to be the ratio L/S , the total number of predator-prey links, L , divided by the total number of species, S . This property, called the linkage density, seems a fairly natural choice, but was also favored by some because analysis of the pre-1990 webs suggested that L/S was independent of S and therefore that this ratio was “scale invariant”. The value of the slope for the best fit to L versus S was found to be 1.99 ± 0.07 , although there appeared to be a slight tendency for the more recently collected webs in that set to have a higher value [9]. The finding that the more recently collected webs tend to be larger, suggests the possibility that the linkage density is not in fact constant, but slightly increasing with S , and that earlier webs were too small to show this clearly. In fact, this was already noted at the time [14, 9, 15]; the scaling relation $L/S \sim S^\epsilon$ with ϵ equal to 0.3 or 0.4 was not ruled out, especially when the sample included larger webs.

An alternative measure of the number of interactions between species, is the connectance, C , of a food web defined as the total number of links in the web divided by the total number of possible links in a web of the same size. Since, excluding links from a species to itself (cannibalism), there are $S(S-1)/2$ possible links in a web of S species, $C = 2L/S(S-1)$. This quantity was originally introduced by theorists [4]-[6], since it is equal to the probability of finding a non-zero entry in the community matrix. Clearly, for large S , the power-law scaling mentioned above gives $C \sim S^{-1+\epsilon}$, with the scale invariance hypothesis leading a hyperbolic S - C relation.

During the 1990’s the scale invariance hypothesis became more and more untenable. The values of the linkage density for the larger post-1990 webs ranged from 3.5 to 11.0, compared with the value of 2.0 found for the pre-1990 webs [16]. The scaling form $L/S \sim S^\epsilon$, with a value of ϵ close to or equal to 0.3 or 0.4 suggested above was still found to be consistent with data [17], although it was also suggested [18, 19] that ϵ might be as large as 1, leading to the conclusion that the connectance was independent of the web size. There are several reasons why the analysis of more recently collected data might differ from the earlier results [20], but an obvious one involves questions of resolution: the earlier webs might be smaller in part because many species and/or links were omitted due to incomplete or biased recording. We will return to this point later in this section, since it is a criticism which may be applied to other measured quantities. Recent work has confirmed that the scale invariance hypothesis for the linkage density is not correct, but no consensus has emerged to replace it. It may simply be that food webs from diverse communities have different characteristics [21], or that while this may be the case, much of the disagreement between data from early webs and those collected more recently can be explained by the fact that the linkage density is very sensitive to sampling effort [22], or that the observed patterns can be explained, but not with simple conjectures as scale invariance or constant connectance [23].

In addition to quantities which describe the structure of the network, such as S and C , it would be useful to have some characterization of the type of species in the web. In order to be meaningful, this should not be so detailed that generic patterns are not seen, but not so coarse that it contains little information. The simplest and most widely used

classification is to divide species in the web up into top, intermediate and basal species. Top species have no predators, basal species have no prey — they obtain all of their resources directly from the environment — and intermediate species have both predators and prey. It is now possible to classify all links in the web into four classes: links between top species and intermediate species, top species and basal species, intermediate species and basal species, and links between intermediate species and other intermediate species. This gives 7 quantities which contain information about the biological aspects of the food-web: the proportions of the species which are top, intermediate and basal (denoted by T, I and B) and the proportion of links between these three types (denoted by, for example, IB , for the proportion of links that go between intermediate and basal species). Only 5 of these are independent, because $T + I + B = 1$ and also the proportion of the links in all four classes add up to unity.

This seems to embody just the right amount of information to allow useful comparison of model webs with real ones. The classification scheme was given further credence when an analysis of the pre-1990 webs suggested that, like L/S , the proportions T, I and B were independent of web size, having values of 29%, 52% and 19% respectively [9]. With L/S and three categories all being independent of web size, it was perhaps not too surprising that the four types of links, TI, TB, IB and II , were also found to be the same in webs of different sizes. The reported values were 35%, 8%, 27% and 30% respectively [9], although, while it is true that the data showed no evidence of increasing or decreasing trends, the scatter of points looked so random that the conceptual jump to the scale-invariance conjecture seemed to be a large one.

As an alternative to the (T, I, B) classification scheme, the proportion of the species which are prey, H , and the proportions which are predators, P , may be used. They are related to the previous set by $H = I + B$ and $P = T + I$. Recall that only two of the set $\{T, I, B\}$ are independent and that $H + P = I + 1$ is greater than unity, since intermediate species are both predators and prey. A frequently quoted statistic for food-webs is the so-called predator-prey ratio (in fact, the prey-predator ratio) H/P . This seems to be the property which shows the least change between the earlier, smaller webs, where it had a value of 0.9, and the more recent, larger webs where it has a mean value only slightly larger than this [16]. There is, however, a considerable spread in actual values for different webs.

The review of food web patterns by Pimm *et. al.* in 1991 [15] was still able to hold on to the belief that many web properties were size-independent, though with high variances and with the possible exception of the linkage density. However, by the time of the next major review in 1993 [16], it was accepted that T, I, B and the links between them did, like L/S or C , vary with the size of the web. This change of view was mainly prompted by two studies [10, 24], which took large food webs and reduced their resolution by lumping more and more of the species together. It was found that many of the quantities discussed above were sensitive to this aggregation. Although the aggregation criteria which were employed were not identical, and thus some of the details of the findings differed, it was clear that generally speaking food-webs properties changed with S . In particular, Martinez [10] found that the highly resolved Little Rock Lake web had larger I , but smaller T and B than the

aggregated version. The fact that the latter had similar properties to the pre-1990 webs, led him to speculate that these webs might too be aggregated versions of larger webs.

These studies were followed up by a re-analysis [25] of an earlier attempt at aggregation [26], which had shown little change with aggregation, and by a re-analysis [27] of the pre-1990 webs [9]. The conclusion of these studies was that aggregated webs and the earlier, smaller webs all have lower L/S , I and II and higher T , B and TB than highly resolved or more recently collected, larger webs. The quantities TI and IB do not seem to change in a consistent way with S . These results can be understood to some degree by beginning with two observations. Firstly, it is now believed that species without any predator are very rare, and perhaps non-existent [10, 28], and thus T will be tiny in well resolved webs. Secondly, basal species are already rather coarsely specified, and it would be difficult to aggregate them further. Thus it might be expected that the proportion of basal species would increase as S decreased. If both T and B decrease as S increases, we would also expect TB to decrease, and I and II to increase. Presumably TI and IB do not change in a consistent direction because, unlike TB and II , they link types of species whose proportions change in opposite directions. For a similar reason, the predator-prey ratio $(I + B)/(T + I)$ seems to be extremely robust under aggregation [16].

These ideas can be extrapolated to the limit by considering a food web with only two species on the one hand, and the entire global ecosystem on the other [29]. While this might be of dubious validity, the trends displayed are suggestive. If the two species web consists of a predator and prey, then $T = 50\%$, $I = 0\%$ and $B = 50\%$. If we assume that the global ecosystem has no, or very few, top species, that animals are intermediate species and plants basal species, and that animals comprise 95% of the species, then $T = 0\%$, $I = 95\%$ and $B = 5\%$. These asymptotic values, taken together with the previous web results, show a consistent trend of T and B decreasing, and I increasing, with S , and the possibility that food web properties become scale invariant for S larger than about 1000 [29]. Studies have also been carried out to investigate other types of sampling effects. For example, the threshold for the inclusion of links can be varied [30, 10] and species can also be omitted (as opposed to being aggregated) [31]. Once again, it was found that the poorly sampled versions of these webs were much more similar to the pre-1990 webs, than were the full versions. Conclusions such as these have convinced ecologists of the need to be more systematic and methodological in the collection of food webs [32]-[34].

What are the other food web attributes which field ecologists should be looking for? In their review, Cohen *et. al.* [9] listed five “laws” of food webs. Three of these dealt with scale-invariance (of the linkage density, of T , I , B , and of the links between these three types). The fourth was that “food chains are short”. A chain in a food web is the set of links along a particular path starting from a basal species and ending at a top species. The number of links along this path is the length of that particular food chain. By averaging this over all the chains in a web, a mean chain length may be assigned to each web. For the food webs listed in [9], the mean chain length over all 113 webs is 2.88 and the median of the maximum chain length in each web is 4 links. The observation that food chains are short is not new;

it is one of the earliest inherent tendencies noted in the study of food webs [35]. The classic explanation is that energy is transmitted very inefficiently up the chain and after dissipation at more than three or four vertices, is not sufficient to sustain predators at the top of the chain [36]. This should mean that productive ecosystems should have longer food chains, but the evidence for this is mixed [8]. Other hypotheses are discussed by Pimm [7]. As for the properties discussed earlier, the nature of food chains in the more recent, larger webs, differ from those appearing in Cohen *et. al.* [9], being typically much longer. This raises the possibility that mean chain lengths are a function of the size of webs. Certainly, food chain length decreases when webs are aggregated [16].

The fifth “law” was that, excluding cannibalism, cycles are rare [9]. Cycles are sets of links which end with the same species as they started from. Of the 113 webs, only 3 contained cycles, and in each case only one cycle of length 2. By contrast the large Little Rock Lake web [10] contained many cycles. If cycles are at all numerous, the definition of the length of food chains given above has to be modified, since it is clearly ambiguous. Two different algorithms were used to calculate food chain length in the case of the Little Rock Lake web. Even when cycle-forming species are excluded, reducing the mean chain length, the mean of 7 links is still much greater than the 2.88 links for the pre-1990 webs.

A term used frequently in ecology is the “level”, or “trophic level” on which a species appears in the food web. This is clearly a useful descriptive term, and when it refers to a single food chain it is obviously unambiguous: it has a value which is one more than the chain length, that is, the number of linkages between it and the basal species in the web [15]. Equally obvious is the fact that it is not a uniquely defined quantity in a web — there will typically be several routes from the species under consideration to basal species. One definition in this case is to list all the possible routes and assign the most common (modal) as the trophic level [7]. Another definition, which seems to us somewhat superior, is to assign the shortest of the possible routes as the trophic level. This choice is based on energy considerations: given the inefficiency of energy transfer along a chain mentioned above, the most important links are likely to be the shortest. This latter definition also has the advantage of being unique; in the former case there may be more than one modal value. While the term “trophic level” is used extensively in a qualitative way in studies of food webs, little is known quantitatively about the number or other attributes of species on different trophic levels, perhaps because of the absence of a single agreed definition. This is unfortunate, because a quantity such as the fraction of the species on a particular level, is relatively easy to obtain from the data and is another attribute which can be compared to models. It is also slightly less coarse than the T, I, B designations, and also probes the food web hierarchy in a slightly different manner; using the latter definition above, basal species are always on level 1, but intermediate species may also be on level 1, and top species need not be on the highest level.

One important property of food webs which rests on the definition of trophic levels is the degree of omnivory. An omnivorous species is one that feeds on more than one trophic level [7]. Thus, for instance, a species which feeds on its prey’s prey is omnivorous. One of the earliest results was that omnivory was less common in some types of real webs, than in randomly

generated webs [7]. About 27% of the species in the pre-1990 webs are omnivores, but the overall picture is quite confused, in part because of the different ways that degree of omnivory can be defined [16]. If the assignments of trophic levels has been agreed upon, the most straightforward index of omnivory is simply the proportion of species which are omnivores. Another measure was given by Goldwasser and Roughgarden [37]. They first determined the statistical distribution of the number of links along all pathways from a particular species to the basal species. The mean of this distribution, which they termed the trophic height, gave a generalized trophic level. The standard deviation, on the other hand, gave an indication of the extent to which the species ate on variety of different levels, and was used by them as a second index of omnivory.

In any case, omnivory seems to be less common towards the base of a community web, and therefore the degree to which sampling favors a particular group of predators will have a marked effect on the percentage of species which are omnivores [16]. Some webs have been reported to have a high degree of omnivory (*e.g.* 78% in [28]), so it is again tempting to list omnivory as another attribute which has been underestimated in the older web data, and in fact it has been found to be sensitive to sampling effort [31]. However, Warren [20] points out that connectance may be a key parameter on which other web characteristics depend, and thus increase in omnivory may not be independent of the increase in connectance. Incidentally, this type of reasoning may be used to argue that more highly connected webs may have a higher proportion of intermediate species (a species is more likely to have links both to it and from it), more cycles, longer chain length and so on.

The description of food webs given so far in this section has focussed on static, structural properties of webs. In reality, food webs are dynamical systems, and links, population sizes, and species composition change with time. This brings additional difficulties into the quantitative description of web structure. Empirical data are collected over a certain time which may vary. If, for instance, a predator feeds on a certain prey only during harsh seasons when other food is scarce, the link to that prey is present only temporarily, and only when links to other prey species are absent. Large food webs, the data for which have been collected over a long time, may therefore overestimate the number of links that are present at a given moment in time.

There are, of course, a wealth of field observations of the dynamical behavior of food webs, but it has not yet been possible to formulate a quantitative, mathematical description that is generally valid across food webs. There are a variety of different population dynamics equations containing different interaction terms, which will be discussed in section 4. The discussion about which mathematical form is more appropriate is lively and diverse.

This section has not been designed to be an exhaustive review of food webs, but rather a summary of the key ideas, concentrating on those that are the most relevant for the modelling of webs. The rest of the article will be devoted to a discussion of the various models of food webs that have been put forward.

3 Static Models

This section describes models that build food webs by assigning links between species according to some rule, and then evaluate the properties of the resulting webs. Species are simply represented as points in space or on a line.

The first such models were modified versions of the random graphs introduced by Erdős and Rényi [38], where links are assigned to randomly chosen pairs of points. Cohen [39, 9] suggested several models for randomly generated webs where links have an orientation indicating which of the two species connected by the link is food for the other one. Links have no orientation in conventional random graphs. Many properties of such directed random graphs can be derived analytically, such as the fraction of top and basal species and the numbers of cycles. The agreement with data from real webs is not very good. This is not surprising, since this simple model has many unrealistic features, such as the assumption that every species can in principle be the predator of every other species.

A model that takes into account the fact that some species are higher up in the food chain than others, has become known under the name “cascade model” [40, 9]. In this model, species are assigned numbers from 1 to S . Each species can prey only on species that have a lower number, and it preys on any of these species with a probability d/S . Here d , the density of links per species, is a constant which, along with S , is the only parameter of the model which has to be fitted to data. One can easily show that the expected number of links in such a food web is $d(S-1)/2$. Therefore, for not too small values of S , the cascade model predicts that the mean number of species should grow linearly with S : $L \sim dS/2$. As discussed in section 2, this is consistent with the pre-1990 webs collected in [9], and with the choice $d = 4$ the mean number of links per species agrees with the then accepted empirical value close to 2. Other properties, such as the fraction of top and basal species, can also be calculated, and they are not far from empirical data for the older collections of webs [9]. For example, the values of T , I and B for large S asymptote to 26%, 48% and 26% respectively when $d = 3.72$. The mean length of the longest chain increases only slowly with the number of species S , and it is around 4 for S between 10^3 and 10^5 . However, the cascade model seems less good at predicting chain length statistics, than many of the other measures investigated [9].

In the light of all of the comments made in section 2 concerning the difference in trends between data collected in the last decade or so and older data, it is not surprising that the predictions of the cascade model have been found to be in disagreement with more recently collected data [18, 37]. Two of the simplest predictions of the cascade model, that food webs are acyclic and that $L \sim S$, are no longer tenable. In an attempt to generalize the cascade model to avoid these and other predictions which are not borne out, Cohen constructed 13 alternative versions of the model [41]. However, in all but one case these were inferior to the original cascade model in predicting general web properties. For example, models which assumed that $L/S \sim S^\epsilon$ with $\epsilon = 0.35$ made inferior predictions to those models which took $\epsilon = 0$. More recent studies have also pointed to deficiencies in the cascade model, especially when the assumption of the random distribution of links is viewed in terms of aggregated

webs [42].

Recently, another static model, called the niche model, was introduced by Williams and Martinez [43]. Just as in the cascade model, the species in this model are put in order: a “niche value” is assigned to them by randomly drawing a number from the interval $[0, 1]$. In contrast with the cascade model, the species are now constrained to consume all prey within a range of values whose randomly chosen center is less than the consumer’s niche value. The size of the range is chosen according to a beta distribution with parameters such that the desired mean number of links per species results. In contrast to the cascade model, species with similar niche values often share consumers, and the strict cascade hierarchy is partially relaxed by allowing up to half of the consumer’s range to include species with niche values higher than the consumer’s value. As in the cascade model there are only two empirical parameters: the number of species and the linkage density (or the connectance). Evaluating 12 different structural properties of the webs generated by the niche model and comparing them to real food web data, the authors found that the agreement between the model web and real webs is in general much better for the niche model than for the cascade model, in particular with respect to features such as cycles and species similarities.

In spite of the apparent success at reproducing properties of real food webs for appropriately chosen parameter values, these static models cannot give a real explanation of the observed web structures. The webs constructed by these models do not result from a dynamical process; links are not assigned according to some biologically inspired rule, and the models do not contain any population dynamics. A good agreement with real data is achieved by capturing some structural features of real webs, but not by incorporating underlying biological properties. In particular, the question of web stability cannot be addressed in these simple models. The question of web stability will be discussed in the next section, where dynamical models are considered, and the question how the structure of webs might follow from evolutionary dynamics combined with biological principles, will be explored in section 5.

4 Dynamic models

The models in the last section attempt to describe food webs as static objects, which is after all what nearly all of the data collected is concerned with. However, it seems more rational to study the kinds of static structures which emerge from biologically reasonable dynamics, rather than attempt to characterize the currently observed webs in terms of simple properties of graphs. As stressed in the Introduction, more than one time-scale will be relevant in food web dynamics; the long time-scale evolutionary dynamics and the shorter time-scale population dynamics will be both important. Evolutionary dynamics will be discussed in the next section. In this section we will review the population dynamics of predator-prey interactions, with greater emphasis on multispecies communities than is traditional in this subject, and with a focus on the question of under which conditions multispecies communities

can be stable.

We will start with a discussion of the two-species model, which is frequently as far as most textbooks go. Then, we will generalize the two-species dynamic equations to an arbitrary number of species. Finally, the stability of such coupled equations for small webs as function of the structural properties of the web, and the types of equations used, will be discussed in subsection 4.3.

4.1 Two-species models

In a two-species model a predator (or parasite) depends for subsistence on a single species of prey (or host) and cannot turn to an alternative food source. We denote the number of predators at time t by $P(t)$ and the number of prey by $H(t)$ (H can be thought of as an abbreviation for “hosts” or “herbivores”). In most cases, these numbers are understood as individuals per unit area, *i.e.*, the predator and prey densities. Almost all of the models which are formulated in terms of differential equations are a special case of what we will call the standard model [44]-[46]

$$\begin{aligned}\frac{dH}{dt} &= \phi(H) - g(H, P) P, \\ \frac{dP}{dt} &= n(H, P) P - d_P P.\end{aligned}\tag{1}$$

Here $\phi(H)$ is the growth of the prey in the absence of predators, $g(H, P)$ is the capture rate of prey per predator, $n(H, P)$ is the rate at which each predator converts captured prey into predator births and d_P is the (constant) rate at which predators die in the absence of prey. The function $n(H, P)$, called the numerical response, which describes how the numbers of new predators relate to the captured prey, is not usually very well known. Frequently it is assumed that a constant fraction of the captured prey are used as resource to produce new predators, that is, $n(H, P) = \lambda g(H, P)$, where λ is a constant called the ecological efficiency. Early models assumed that the growth rate of an individual prey in the absence of predators was constant, that is, $\phi(H) = rH$, but most models now include intra-species competition by taking $\phi(H)$ to have the logistic form $\phi(H) = r(1 - H/K)H$, where K is the carrying capacity. With these choices, the type of model is specified solely by the choice of the function $g(H, P)$, called the functional response.

The first model of predator-prey dynamics put forward having the form (1) was the Lotka-Volterra model which had exponential (not logistic) growth of the prey ($\phi(H) = rH$) and a linear functional response $g(H, P) = aH$, so that the capture rate for an individual predator increased linearly with the number of prey [45]. This model has the unrealistic feature of neutral stability: it contains a limit cycle with an amplitude which is determined by the initial conditions, rather than by the parameters of the model. Imposing a logistic form for $\phi(H)$ cures this, but only by eliminating limit cycles entirely [46]. During the 1960’s the study of the standard model (1), with more realistic forms for the functional response began.

Rosenzweig and MacArthur [47, 48, 44] developed a graphical method to determine what functional forms for g and ϕ gave rise to stable fixed points and limit cycles, although the analysis was restricted to functions g which only depended on H , and not on P . A broad conclusion was that the most complete range of behaviors were seen in (1) if $\phi(H)$ had the logistic form and if $g(H)$ saturated at some constant value for large H (the so-called Type II form).

A specific Type II functional form suggested by Holling [49] is widely used in modelling, partly because of its simplicity, but also because it can be derived in a reasonably convincing way [50]. The essential idea is that the period of searching, T , should be divided into true searching time, T_s , and a “handling time”, T_h , which represents the time taken to eat the prey as well as the time taken afterwards to clean, rest and digest the food. Use of T_s , rather than T , in the definition of the functional response, and the assumption of random encounters between predators and prey, gives the Holling form

$$g(H) = \frac{aH}{1 + bH}, \quad (2)$$

where a and b are constants. Beddington [51] extended this idea by having a second type of “wasted time” in addition to the handling time, namely time wasted when two predators meet. Incorporating this into the definition gave a functional response which depended on the number of predators:

$$g(H, P) = \frac{aH}{1 + bH + cP}, \quad (3)$$

where c is another constant. Both forms (2) and (3) are widely accepted as reflecting essential features of predator-prey interactions. However, this acceptance is not universal, and the traditional arguments used to construct them have been criticized [52]. The basis of the criticism is that the function g appearing in the population dynamics equations should be the function calculated on the same time scale as that of the population dynamics, and not that calculated on the same time scale as the behavioral response. When viewed from the slow time scale, prey abundance is assumed to appear as a continuous function. However, when viewed from the fast behavioral time scale, prey production is no longer continuous but appears as successive “bursts”. Between these bursts, the predators consume the prey (or the fraction of prey available to predation) by some mechanism (possibly random search). Thus, for a given number of prey, each predator’s share is reduced if more predators are present. This suggests that the consumption rate should be a function of prey abundance *per capita*, that is,

$$g(H, P) = \Phi(H/P), \quad (4)$$

a ratio-dependent functional response. The form of the function Φ can be deduced by looking at two extreme situations. When the prey is very abundant, predators feed at a constant maximum rate, so that $\Phi \rightarrow \text{constant}$, for $H \gg P$. On the other hand, if predators are very abundant they will consume prey at a constant rate, so that $g(H, P)P = a'H$ in the limit

$H/P \rightarrow 0$. A simple form which has this structure is

$$g(H, P) = \frac{a'(H/P)}{1 + b'(H/P)} = \frac{a'H}{P + b'H}. \quad (5)$$

Beddington's form and this specific form of the ratio-dependent functional response may be written as

$$g(H, P) = \frac{H}{\alpha + \beta H + \gamma P}, \quad (6)$$

where α, β and γ are constants. The only difference is that in the ratio-dependent case $\alpha = 0$. Despite these similarities, there has been a vigorous discussion in the literature as to the superiority of one form over the other [53]-[58]. The essential differences between the two methods of modelling the functional response are discussed in a recent review article written by authors from both camps [59].

4.2 Generalized dynamical equations

The generalization of the population dynamics equations (1), with realistic growth rates ϕ and functional responses g , to more than two species is straightforward for a food chain [60], or other simple webs, such as two chains with a mobile top predator [61], but less obvious for a general web. For this reason virtually all investigators, starting with May [5], who have studied the population dynamics for a general web have used Lotka-Volterra dynamics. However the well-known unsatisfactory features of these equations [6], together with a desire for greater realism, have resulted in some suggested versions of population dynamics which go beyond the Lotka-Volterra scheme [62]-[66].

Let us begin with the Lotka-Volterra equations. If N_i is the population size or population density of species i , the Lotka-Volterra equations for a general web may be written as

$$\frac{dN_i(t)}{dt} = N_i \left(b_i + \sum_j a_{ij} N_j \right), \quad (7)$$

where b_i is a positive growth rate for basal species, and a negative death rate for the other species. The b_i and the interaction coefficients a_{ij} are constants, independent of the population sizes. There are three different possible contributions to $\sum_j a_{ij} N_j$: (i) As mentioned in the context of two-species models, many authors include a logistic term for the basal species, implying $a_{ii} < 0$ for basal species, and zero for the other species. (ii) Some authors using Lotka-Volterra models include competition between two predators that share the same prey, *i.e.*, $a_{ij} < 0$ whenever i and j have a prey in common. (iii) The most important contributions are the predator-prey terms. If i is a predator and j is one of its prey species, then $-a_{ji} N_j$ is the functional response g_{ij} , *i.e.*, the number of individuals of species j consumed per unit time by an individual of species i . Often, the identity $-a_{ji} = \lambda a_{ij}$ is used, but some Lotka-Volterra

models have independent random (positive) numbers for a_{ij} and $-a_{ji}$, and some models do not even impose opposite signs for a_{ij} and a_{ji} .

We will restrict our discussion of general non-Lotka-Volterra type equations to those that satisfy the balance equations

$$\frac{dN_i(t)}{dt} = \lambda \sum_j N_i(t) g_{ij}(t) - \sum_j N_j(t) g_{ji}(t) - d_i N_i(t). \quad (8)$$

These equations are in many ways the natural generalizations of (1), with the first term on the right-hand side representing the growth in numbers of species i due to predation on other species, the second term the decrease in numbers due to predation by other species, and the last term the constant rate of death of individuals of species i , in the absence of interactions with other species. Where there is no predator-prey relationship between species i and species j , g_{ij} is zero. There are two minor variants on (8): the basal species may be treated differently from the other species, and given a positive growth term to represent feeding off the environment, or the environment may be included as a “species 0” and these growth terms represented by functional responses g_{i0} .

Apart from the constant death rates d_i and the ecological efficiency, λ , the model is completely specified once the functional responses have been chosen. Arditi and Michalski [65] have pointed out that these generalized functional responses, if they are to be logically consistent, must leave the balance equations invariant if two identical species are aggregated into a single species. The obvious generalized form of the Holling type functional response, Eq. (2), is

$$g_{ij} = \frac{a_{ij} N_j}{1 + \sum_k b_{ik} N_k}, \quad (9)$$

where the sum in the denominator is taken over all prey k of species i .

Generalizations of more complicated functional responses can only be found in the recent literature. Arditi and Michalski [65] suggest the following generalized Beddington form:

$$g_{ij} = \frac{a_{ij} N_j}{1 + \sum_k b_{ik} N_k + \sum_l c_{il} N_l}, \quad (10)$$

where the first sum is again taken over all prey k of species i , and the second sum is taken over all those predator species l that share a prey with i .

A possible generalization of the ratio-dependent functional response results from Eq. (10) if the 1 in the denominator is cancelled. However, as Arditi and Michalski [65] point out, the idea that predators share the prey, which led to the introduction of ratio-dependent functional responses, is better reflected by the following expression,

$$g_{ij} = \frac{a_{ij} N_j^{r(i)}}{N_i + \sum_{k \in R(i)} b_{ik} N_k^{r(i)}}, \quad (11)$$

with the self-consistent conditions

$$N_j^{r(i)} = \frac{\beta_{ji} N_i^{C(j)} N_j}{\sum_{k \in C(j)} \beta_{jk} N_k^{C(j)}}, \quad N_k^{C(j)} = \frac{h_{jk} N_j^{r(k)} N_k}{\sum_{l \in R(k)} h_{lk} N_l^{r(k)}}.$$

Here β_{ij} is the efficiency of predator i at consuming species j , h_{ij} is the relative preference of predator i for prey j , $R(i)$ are the prey species for predator i , $C(i)$ are the species predating on prey i , $N_j^{r(i)}$ is the part of species j that is currently being accessed as resource by species i and $N_k^{C(j)}$ is the part of species k that is currently acting as consumer of species j . An interesting consequence of this implicit form of the functional response is that not all the links that are in principle possible are realized, by a long way. This is a very realistic feature of the model, since species typically feed on those prey that are most easily available, and resort to other prey only during periods of food shortage. Arditi and Michalski [65] also found that small food webs with this generalized ratio-dependent functional response are far less sensitive to the aggregation of species than webs with prey-dependent functional responses.

A shortcoming of model (11) is that the predator preferences h_{ij} are constants that are independent of prey availability. In reality, one can expect that predators assign more effort to those prey from which they obtain more food per unit effort, so that a stationary point is reached only when a predator obtains from each prey the same amount of food per unit effort. This condition is implemented in the generalized ratio-dependent functional response suggested by Drossel, Higgs, and McKane [66], Eq. (13), which is discussed in the next section.

4.3 The complexity-stability debate

So far in this section we have surveyed the kinds of population dynamics equations which are frequently applied to the modelling of predator-prey systems. As is usual, we have assumed that the parameters of the various models are given, but for a large community these may be hundreds in number. Obviously some way of specifying the parameters is required, and it is at this stage that we move into the question of food-web modelling, since many of these parameters will be related to the underlying web structure. The methods that have been used to go beyond pure population dynamics to incorporate food-web structure fall into three classes (see, for instance, [67], who defines the first two classes). The first class, which is the object of this subsection, studies the stability of small webs as function of their structure, of the choice of dynamic equations, or of the choice of parameter values. The motivation for this type of study is the intuition that real food webs must be stable. Part of this program involves defining exactly what is meant by “stable”. The second class, which will be studied in section 5.2, assembles communities from a very small original system by bringing in species from a “species pool”, and if they can add to the community in a stable way, they are incorporated into the system. In this way, larger ecosystem can, in principle, be built up. Third, in evolutionary models (see section 5.3), a community is built up not from a preexisting pool of species, but by modification (“mutation”) of existing species.

The first attempt to write down mathematical equations for the dynamics of food webs and to study their stability, is due to May [5]. May performed a linear stability analysis of the population sizes around a supposed equilibrium point:

$$\frac{d}{dt}(\delta N_i) = \sum_j \alpha_{ij} \delta N_j, \quad (12)$$

where δN_i is the deviation of the population size of species i from its equilibrium value and α_{ij} is the community matrix. In this way he avoided specifying the underlying population dynamics equations, but was constrained to stay near equilibrium. The choice of web structure is equivalent to the choice of the α_{ij} . May chose the diagonal elements of the matrix to be -1 . The other elements were taken to be zero with probability $1 - h$. With probability h , they had a random nonzero value chosen from a distribution of width α , so that α is a measure of the average interaction strength. Using results from random matrix theory, he found that ecosystems that are initially stable will become less stable (*i.e.*, the initially negative eigenvalues of the community matrix move towards zero) when $\alpha(SC)^{1/2}$ is increased. Furthermore, Eq. (12) will almost certainly be stable if $\alpha(SC)^{1/2} < 1$, and almost certainly be unstable if $\alpha(SC)^{1/2} > 1$. This finding spurred on much of the interest in the relationship between C and S discussed earlier. The belief that webs with high connectance were unstable supplied a reason why webs with large C were not observed. On the other hand, the result was hard to reconcile with the increasing evidence for the scaling relation $C \sim S^{-1+\epsilon}$, $\epsilon > 0$ unless α was very small, there were complaints from field ecologists that the webs which they had been observing for many years should be unstable according to the May criterion [28], and there were discussions concerning the mathematical basis of the result [68]-[70].

Although May's work was interesting because it broke new ground, there were obviously several weak points in the analysis. One was the lack of biological realism assigned to the web. It was argued that the web structure should be "plausible", and not just randomly generated [71, 72]. It was suggested, for example, that food webs with "realistic", rather than random, structures had more chance of being stable [72]. These ideas were made more concrete by Yodzis [73], who constructed "plausible community matrices" by using the topologies of real webs, with the correct sign and an estimate of the magnitude of the strength of the links. He then showed that in every case where community matrices were plausible, disrupted forms of these matrices, which no longer represented real communities, were less stable. Other authors [74, 75] started with a large random Lotka-Volterra system (of the order of 50 species) and successively removed those species that were least stable, until a stable smaller food web was obtained, which typically had more positive coefficients than random networks. Still other authors investigated the stability of small Lotka-Volterra food webs (typically 4 to 10 species) as a function of the connectivity pattern and the link strengths. For Lotka-Volterra systems, one simply has $\alpha_{ij} = N_i^* a_{ij}$, where N_i^* is the equilibrium population size of species i . Taking into account differences in body size between predators and their prey, Pimm and Lawton [76] found that webs with more omnivory (*i.e.*, more links) are not always less likely to be stable. The exception occurs in webs where a "predator" is a small parasite i of a large host, j , in

which case $|\alpha_{ij}|$ is much larger than $|\alpha_{ji}|$. De Angelis [71] found that small webs are more stable when the ecological efficiency λ is smaller, when species on higher trophic levels have strong self-limitation (*i.e.*, a strong negative a_{ii}), or when the predator population dynamics have little impact on their prey.

Very recent evidence suggests that models with more realistic functional responses tend to be more stable than Lotka-Volterra systems. In those models, the community matrix α_{ij} has no simple relation to the coefficients in the dynamical equations, and its values can therefore be expected to be far from random, even if the parameters in the dynamical equations are chosen in some random way. This was demonstrated explicitly by Pelletier [77], who studied a system of n basal species (prey) and n predator species feeding on these prey, choosing a functional response of the form

$$g_{ij} = a_{ij} N_j \frac{na_{ij} N_j}{\sum_k a_{ik} N_k}.$$

In this way, a predator can assign more weight to a prey from which it obtains more food. Pelletier found that 85% of these types of food webs (with random values for a_{ij}) are stable, irrespective of the value of n , in contrast to Lotka-Volterra systems, where the percentage of stable webs decreases quickly with n . We will see in the next section that an evolutionary model that uses generalized ratio-dependent functional responses, can build larger food webs than a Lotka-Volterra type model, indicating again that Lotka-Volterra systems are less stable than more realistic ones.

Another weak point of May's analysis is the use of linear stability analysis. Clearly, a model ecosystem need not be at a stable equilibrium point in order to be realistic, but may instead be on a limit cycle or even a chaotic trajectory, as long as the fluctuations are small enough that no species get close to extinction. In such a situation, the question as to whether more complex ecosystems are more stable takes the form "under what conditions have more complex systems smaller fluctuations in population sizes". Intuitive arguments were put forward that the addition of weak links to an existing web with a strong predator-prey coupling should have a dampening effect on the population oscillations of the strongly coupled predator-prey pair. The reason is that the predator can feed on an alternative prey to which it has a weak link when its main prey becomes low in population size, allowing the main prey to recover. Similarly, a weakly linked alternate predator can increase in population size when the main predator decreases, thus preventing a large oscillation in prey population. These arguments are supported by the numerical study of models for small food webs with several weak links. Using a Holling-type generalized functional response, McCann, Hastings, and Huxel [78] found that the weak links have indeed a stabilizing effect on the model dynamics. Polis [79] suggests that the chosen form of the functional response is important for the result, since it makes it impossible for a predator to maintain a high feeding efficiency on many prey at the same time (in contrast to Lotka-Volterra systems). Field data seem to support the hypothesis that stable food webs have many more weak links than strong links [78].

Some authors point out that species rich communities should have less community-level variability (*i.e.*, relative fluctuation of the combined density of all species sharing the same ecological role) than species poor communities, where the oscillations of one species cannot be counterbalanced by different oscillations of another species. This concept of community-level stability is supported by numerical simulation of a Lotka-Volterra type model [80], and is reviewed by Loreau in [81].

An alternative definition of stability, called “species deletion stability”, which might have more direct relevance to real webs was introduced by Pimm in 1979 [82]. An ecosystem is defined to be species deletion stable if, when a species is removed from the web, all the remaining species remain at a stable equilibrium involving only positive densities. Species deletion stability decreases with increasing numbers of species and connectance, *i.e.*, decreases with complexity [82], but it also depends crucially on which species are selected for removal [83]. A quantitative measure of the deletion stability of a web is provided by S_d , the fraction of species for which the web is species deletion stable. However, it should be noted that data on experimental species removal show that many real species are not species deletion stable [83]. Recent work [84] showed that the risk of additional species deletions, following the loss of one species in model food webs, decreases with biodiversity. A review of the relation between the complexity and stability of an ecosystem [85] concluded that much of the confusion in the literature to date arose because of the different meanings given to the terms “complexity” and “stability”; many different definitions of perturbations and persistence are possible, and only a few are appropriate for real webs. One of the more fruitful of these has been the idea of “permanence” [86, 87], which will be explored in more detail in the following section, when assembly models are discussed. Recently the diversity-stability debate has been reviewed by McCann [88].

5 Assembly models and evolutionary models

This section describes models for food webs which incorporate longer time scales. In contrast to the models presented so far, they allow for the ongoing introduction of new species (due to immigration or speciation) and for species extinctions. As a consequence, the composition and structure of the web changes with time. Studies of assembly models and evolutionary models focus mainly on the features of the food web after a sufficiently long time, when the size of the food web and other properties cease to change in a systematic manner.

While the static models presented in section 3 are only concerned with web structure, but cannot address web stability, and while the dynamic models presented in section 4 focus on the stability of web subunits but do not deal with the overall web structure, the models presented in this section combine the two aspects of web structure and web stability. Another advantage of assembly models and evolutionary models is that links between species and interaction strengths are shaped by the web’s history, instead of being assigned in an ad-hoc manner as in the other two types of models.

Assembly models and evolutionary models can be divided into three classes, which will be presented in the following subsections. The first class comprises toy models that resemble to some extent the static models discussed in section 3. They ignore population sizes, and species, and links are added and removed according to simple rules. The structure of the resulting webs is usually different from the structure of real food webs, as described in section 2. However, the main focus of these models is on species extinctions rather than on the food web structure, and these extinction events bear some similarity to those seen in the fossil record [89].

The other two classes of models are more realistic, as they take population sizes into account and include such important features as competition for food and link strength, which are not part of the toy models. The second class of models are species assembly models, which, starting from a small initial system, bring in new species from a species pool that are incorporated in the system if they add to the community in a stable way. These species assembly models, which typically lead to an uninvadable, stable system, will be discussed in subsection 5.2. The third class of models, reviewed in subsection 5.3 are inspired by biological evolution through modification of existing species. Just as the assembly models, they start from a small set of species, and then add new species, which are obtained by modifying existing species. In spite of differences in the population dynamics, the different evolutionary models lead to similar and realistic food web shapes.

5.1 Toy models

The purpose of introducing evolutionary toy models was not so much to reproduce realistic web structures, but rather to study the large-scale dynamics of species extinctions. Species are usually characterized by a number which is related to their fitness, and they become extinct when this number falls below a threshold value. The web structure can be a regular lattice, as in the Bak–Sneppen model [90], or a fully connected web, as in the Solé–Manrubia model [91], or new links are added together with a new species according to some rule, as in the Slanina–Kotrla model [92] and the Amaral–Meyer model [93]. Fitness changes are triggered by changes in species linked to a given species, and they also include a stochastic component. An overview of all these models was given by Newman and Palmer [94] and by Drossel [95].

Since the links in these models are in most cases not understood to be feeding relations but interactions of any type, their connection to food webs is only superficial. In the following, we give a description only of the model by Amaral and Meyer, which is the one closest to food webs, since it places the species in trophic layers, with links indicating which species feeds on which other species. The model is defined as follows: Species can occupy niches in a model ecosystem with L levels in the food chain, and N niches in each level. Species from the first level $l = 0$ do not depend on other species for their food, while species on the higher levels l each feed on k or less species in the level $l - 1$. Changes in the system occur due to two processes: (i) Creation of new species with a rate μ for each existing species. The new species becomes located at a randomly chosen niche in the same level or in one of the two

neighboring levels of the parent species. If the new species arises in a level $l > 0$, k species are chosen at random from the layer below as prey. A species never changes its prey after this initial choice. (ii) Extinction: At rate p , species in the first level $l = 0$ become extinct. Any species in layer $l = 1$ and subsequently in higher levels, for which all preys have become extinct, also become extinct immediately. This rule leads to avalanches of extinction that may extend through several layers. Amaral and Meyer found from computer simulations that the size distribution of these extinction avalanches is given by a power law $n(s) \sim s^{-\tau}$ with $\tau \simeq 2$. This result $\tau = 2$, which was confirmed by an analytical calculation by Drossel [96], is compatible with the findings of paleontologists that species extinction events of all sizes have occurred in the geological past [89]. A more detailed study which also includes the taxonomy generated by the model is given by Camacho and Solé [97].

Large extinction avalanches are also found in the other toy models mentioned above, and they imply that the internal dynamics of ecosystems place them at the border of stability such that small triggers can have large consequences. However, the more widely accepted view seems to be that ecosystems in themselves are rather stable, but that external events like meteorite impacts or changes in the sea level are to blame for the large extinctions in the geological past. If this is correct, the simple toy models miss important ingredients that are present in real ecosystems. The more realistic models described in the next subsection lead to food webs that are much more stable.

5.2 Species assembly models

The more realistic assembly and evolutionary models, which will be discussed in the remainder of this section, include population dynamics. They have two time-scales, which are assumed to be separated. On the faster, ecological time scale, population sizes change until they reach fixed points or stationary orbits. On the slower time scale, new species are introduced by immigration (assembly models) or by modifying one or a few individuals of an existing species (evolutionary models). After introduction of the new species, the population dynamics may either drive this new species to extinction, or the new species becomes established, while possibly one or a few other species become extinct. Even if no species become extinct, the food web may become rearranged, with species abandoning one prey or choosing an additional prey.

Species assembly models take into account that real ecosystems, for instance on an island, are often built up by species immigration. Starting with either one or a few species, species from a “species pool” are added to the system, and they remain in it if the resulting system is stable. Energetically constrained community assembly was modelled by Yozdis [73, 98]. Starting with N basal species each of which has a “production” P , new species are introduced one by one. The required energy intake e of a new species is chosen from a given probability distribution, and the prey species are chosen one by one with probabilities proportional to their unused production. If a prey has a randomly chosen fraction of its production available, this prey is utilized by the new species, and further links to preys are added until the energy

needs of the new species are satisfied. The assembly process ends when the total unutilized production falls below a minimum value. The resulting webs have properties that agree well with real web data.

In all the other models, population dynamics is modelled via Lotka-Volterra equations. The species pool is usually a set of no more than 25 basal species (“plants”), and the same number of “herbivores”, “carnivores” and top predators, with interaction coefficients between neighboring layers assigned according to some random rule (sometimes taking the larger body size of consumers into consideration or trying to include “specialists” that feed on only one prey as well as “generalists” that can feed on several prey). The third or fourth trophic level (carnivores and top predators) are missing in some of the models. Although this species pool is usually interpreted as stemming from a large ecosystem, like the mainland, no stability criteria or other criteria inspired from real large webs are applied to it.

After adding a new species with an initially small population size to the system, one of the three following things can happen: (i) The new species increases and coexists with all the other species. (ii) The new species remains in the system, but one or more other species go extinct. (iii) The new species goes extinct. Numerical integration of Lotka-Volterra equations, combined with the criterion of local stability, were used by Post and Pimm [99] and by Drake [100, 101], to construct webs of typically less than 20 species. Since the numerical integration of large Lotka-Volterra systems is very inefficient [102], other authors [103, 104] use the concept of permanence in order to find the composition of the new community after species addition. An ecological community is permanent if all species remain at a positive finite density when the density of each is started at a positive finite value. For Lotka-Volterra systems, the permanence of a system can be quickly tested using only two criteria. Clearly, this criterion of permanence is too strict, since real systems never explore the full space of possible population sizes, and since it seems implausible that for real communities even very unusual combinations of population sizes should not result in species extinctions.

After some time, an invasion-resistant state is achieved, the properties of which can be evaluated as function of the properties of the species pool. The invasion-resistant state may be a single community, or (in a minority of cases) a cyclic sequence of communities. Typically, the size of the resulting community increases with the size of the pool, but saturates when the pool size becomes large [104].

Lockwood *et al* [105] showed that if subsequent invasions follow rapidly (instead of waiting for a stable species configuration after each invasion), before the system can achieve an equilibrium state, communities do not evolve towards an invasion-resistant state, but move through complex cycles of composition, where each species gets its turn. A recent review on community assembly, with the main focus on phenomenology rather than models, is [106].

To summarize, the species assembly models put forward so far are capable of generating intermediate-size webs with a predetermined number of trophic layers. There are several drawbacks of these models. First, so far only Lotka-Volterra equations have been used. However, since equations using other functional responses are known to be more realistic and more stable, it would be worthwhile to investigate species-assembly models with other functional

responses. Second, the species pool is not very large, thus limiting the number of possible modifications of the web. It might well be possible that with a much larger pool, the webs would not evolve towards an invasion-resistant state. Third, the species pool is composed of random species. Since the assembled web will consist after some time of species that are in some respect adapted to each other, it is very unlikely that a randomly defined additional species could invade the system. In contrast, real species pools contain species that have evolved to be able to survive well in the presence of other species from the pool. A real species pool, even when not large, will therefore contain many more species that can invade the ecosystem under consideration, than do the random species pool used in the models. The evolutionary models presented in the next subsection have no species pool at all, but they introduce new species as modifications of existing ones. New species are therefore much more likely to fit into the existing ecosystem than the randomly generated species in assembly models.

5.3 Evolutionary models

Evolutionary food web models introduce new species as variations of existing ones. The first evolutionary food web model that includes population dynamics was introduced by Caldarelli, Higgs and McKane [107]. Species in this model can be characterized as binary strings, with each bit representing a feature that is either present (1) or absent (0) in a species. This representation gives a measure of similarity between species (the number of features they have in common) and allows for “mutations” by randomly swapping a 1-bit and a 0-bit (*i.e.*, by replacing one feature with another). “Scores” between two species are obtained by multiplying the two feature vectors to the right and left of an asymmetric random matrix that is chosen at the beginning of the simulation. Positive scores indicate that the first species can feed on the second species, and negative scores mean that the first species is eaten by the second. The external resources are represented as an additional species of fixed (and large) population size, which does not feed on any species. The population dynamics are simple: at each time step, a fixed percentage of every species that has at least one predator is eaten by the predators of that species. The prey is divided such that all those predators that have a score within a certain narrow range of the maximum score against a prey species obtain a share, the size of which depends linearly on the score. This means that species do not feed on all prey species they can potentially feed on. As the web changes and evolves, the prey species eaten by a given predator can change. Since the dynamical equations are linear, they quickly reach a fixed point. Then, a randomly chosen individual is “mutated”, and the new population sizes are calculated. Starting with one species and the external resources, large webs can be built. After some time, a stable species configuration is reached such that no “mutant” can become established. The parameters of the model can be chosen such that the fractions of top and bottom species, the numbers of links per species and other properties of the webs are very similar to those of real food webs.

In a subsequent paper by Drossel, Higgs and McKane [66], a modified version of this

model was introduced, which contains more realistic population equations. For all species equations of the form Eq. (8) were used. As in the previous model, $\lambda = 0.1$ was chosen, and the external resources were modelled as an additional species with a large and fixed population size. Apart from the external resources, all species have a death rate $d_i = 1$ and a ratio-dependent functional response of the form

$$g_{ij}(t) = \frac{S_{ij}f_{ij}(t)N_j(t)}{bN_j(t) + \sum_k \alpha_{ki}S_{kj}f_{kj}(t)N_k(t)}. \quad (13)$$

The S_{ij} are the above-mentioned scores, and f_{ij} is the fraction of its effort (or available searching time) that species i puts into preying on species j . These efforts must satisfy $\sum_j f_{ij} = 1$ for all i , and they are determined self-consistently from the condition

$$f_{ij}(t) = \frac{g_{ij}(t)}{\sum_k g_{ik}(t)}. \quad (14)$$

This condition is such that no individual can increase its energy intake by putting more effort into a different prey. The parameters α_{ki} give a measure of the strength of competition between species k and i . They are equal to 1 for $i = k$, and a linear function of the overlap between species i and k (*i.e.*, of the number of features that i and k have in common) for $i \neq k$.

In computer simulations of the model, the population sizes quickly reach a fixed point. As discussed in the previous section, this is generally not the case for Lotka–Volterra type population dynamics. The effects of competition, of predator saturation, the ratio-dependent functional response, and the ability to assign more effort to searching for the better prey species, may all play a crucial role in stabilizing the population dynamics. Using the same evolutionary dynamics as in the previous model, large food webs can again be built that consist of several hundreds of species. Just as with the simpler population dynamics equations of the previous model, the properties of the food webs agree well with the empirical ones. In contrast to the above model, which has simpler population dynamics, no stable species configuration is reached, but there is ongoing species creation and extinction, even after a long time. However, no more than a few species become extinct at the same time, and the size distribution of extinction events has a sharp exponential cutoff. The evolutionary dynamics of the model, combined with the population dynamics, thus create large stable webs, which have ongoing changes due to species overturn, but do not show strong responses to small perturbations. More recent studies of this model can be found in [108, 109]. Figure 2 shows an example of a food web generated by this model.

A different dynamical model, which uses Lotka–Volterra type equations, was introduced by Lässig *et al* [110]. In contrast to standard Lotka–Volterra equations, where the quadratic term is only used for predator–prey relationships, these authors also include a predator–predator competition term. The a_{ij} in Eq. (7) are equal to a constant γ_+ if j is predator of i , and $-\gamma_-$ (with $0 < \gamma_- < \gamma_+$) if i is predator of j . If i and j have a prey in common, then a

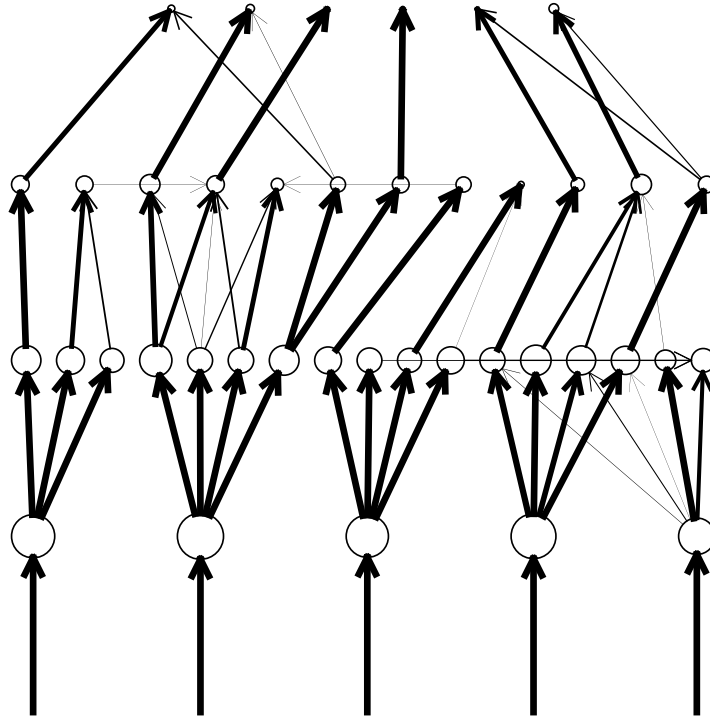


Figure 2: Example of a food web generated by the evolutionary model [66]. The radius of the circles is proportional to the logarithm of the population size, and the thickness of a link is a measure of the energy flow along that link.

competition term is added to a_{ij} , which is -1 for $i = j$ and $-\beta\rho_{ij}$ otherwise, with β being a constant smaller than 1, and ρ_{ij} the link overlap between the two species, which is defined as the geometric mean between the fraction of i 's prey species that it shares with j and the fraction of j 's prey species that it shares with i . All species have the same death rate. The external resources are represented as a few species with a positive growth rate and no prey.

The “mutations” which generate the evolutionary dynamics in this model consist in a change of a predation link for an individual. Using a mean-field approximation, the authors analyzed this model analytically and obtained web structures which are very similar to realistic food webs. Computer simulations of this model are given in [111]. However, up to now only simulation results for one trophic layer of species have been published. All these species feed on the external resources, which are modelled as permanent species with a constant growth rate. The computer simulations show a constant turnover of species, with considerable fluctuations in the total number of species. This is in strong contrast to model [66], where simulations of one trophic layer always converged to an uninvadable species constellation. This confirms again the finding that Lotka-Volterra systems are less stable than systems with more realistic functional responses. It would be interesting to see how the model [110] behaves if several trophic layers are allowed. We expect that it would be less stable and that the webs would be smaller than for model [66].

The fact that the different evolutionary models give the same overall structure of the food web, indicates that the shape of food webs results from a few general principles, and is not much affected by certain details of the system. All models include competition between predators, and an efficiency of converting eaten prey into predator biomass which is smaller than 1. Furthermore, there are only few different external resources. Qualitatively, one can understand how these ingredients generate the familiar food web shapes: one can argue that very few external resources, combined with competition among the species feeding on these resources and with predation allowing only efficient feeders to survive, leads to only a few basal species that feed on these resources. Since there are more basal species than different external resources, there are more predator species that can coexist feeding on the basal species. The number of species thus increases initially with increasing trophic level, until the total biomass becomes so small that only a few top species can survive at the highest level. This explains the short length of food chains and the small proportion of basal and top species. The small number of links per species must result from the competition between predators, the strength of which can be tuned in all of the models.

6 Conclusions

Our aim in this review has been to survey most of the approaches that have been used to model food webs and to discuss real web data in enough detail to provide a background to the model building. A number of clear trends can be seen in both theory and experiment. In the latter case there has been a realization in the last decade or so that data collection needs to

become a much more controlled and systematic affair. Much of the older data was collected as a by-product of other projects, and it has become clear that the database of collected webs contains enough hidden biases to raise serious doubts about its usefulness. Recently food web data has been far more painstakingly collected, and has been done as part of projects specifically devoted to the investigation of food webs. Eventually the quality of the ensembles of collected webs will reflect this. The theory of food web structure has also made advances during this time. Much of the early work concerned webs with random, rather than evolved, structures, but there has been a tendency in later work towards building up a web either from a pool of species (assembly models) or, more recently, by creating webs through modification of the existing species (evolutionary models). In parallel with these developments, some suggestions for more realistic population dynamics for whole communities, and not just for a single predator-prey pair, have been put forward. In our opinion these last two developments, taken together, will form the basis for further progress in the theory of food webs.

We have seen that evolved food webs or webs generated through a series of species invasions are generally more stable than randomly assembled food webs, even if realistic food web shape is imposed. Large and complex randomly assembled food webs simply collapse under the population dynamics and are very unlikely to be stable. Evolutionary dynamics can choose the predator-prey links and the competition structure such that stable webs are built step by step, starting from a small initial web. We do not yet know in sufficient detail in what respects the link strengths and link structure of evolved networks differ from ad-hoc compositions.

Furthermore, there is a need to investigate the effects of different functional responses on the structure and stability of food web models, rather than continuing to use the less satisfactory Lotka-Volterra equations. In section 4 we drew attention to the existence of theories of population dynamics with realistic functional responses which can be applied to communities with arbitrary structures. The amount of computer time required to construct model webs will not obviously be much greater than using Lotka-Volterra equations, and there will probably be a saving due to the increased stability of the models with more realistic functional responses.

To conclude, we hope that more realistic functional responses will be used to investigate the structure and stability of assembled and evolved webs in greater depth in the future, and that models will be constructed that create webs by both immigration from a species pool and by variation of the species within the community. We believe that these, and other similar studies, will pave the way for a greatly increased understanding of the structure and nature of food webs over the next few years.

Acknowledgements

We thank C. Quince for producing Figure 2. B.D. was supported by the Deutsche Forschungsgemeinschaft (DFG) under Contract No Dr300-2/1.

References

- [1] E. P. Odum, *Fundamentals of ecology*, (Saunders, Philadelphia, 1953).
- [2] C. S. Elton, *Ecology of Invasions by Animals and Plants*, (Chapman and Hall, London, 1958).
- [3] R. H. MacArthur, *Fluctuations of animal populations and a measure of community stability*, Ecology **36** (1955), 533–536.
- [4] M. R. Gardner and W. R. Ashby, *Connectance of large dynamic (cybernetic) systems: critical values for stability*, Nature **228** (1970), 784–784.
- [5] R. M. May, *Will a large complex system be stable?* Nature **238** (1972), 413–414.
- [6] R. M. May, *Stability and complexity in model ecosystems*, (Princeton University Press, Princeton, 1974), Second edition.
- [7] S. L. Pimm, *Food webs*, (Chapman and Hall, London, 1982).
- [8] J. H. Lawton, *Food webs* in *Ecological Concepts*, J. M. Cherrett, (ed.), (Blackwell, Oxford, 1989), pp 43–78.
- [9] J. E. Cohen, F. Briand and C. M. Newman, *Community food webs*, Biomathematics Vol. 20, (Springer-Verlag, Berlin, 1990).
- [10] N. D. Martinez, *Artifacts or attributes? Effects of resolution on the Little Rock Lake food web*, Ecol. Monogr. **61** (1991), 367–392.
- [11] M. Huxham, S. Beaney and D. Raffaelli, *Do parasites reduce the chances of triangulation in a real food web?* Oikos **76** (1996), 284–300.
- [12] D. P. Reagan and R. B. Waide, *The food web of a tropical rain forest*, (U. of Chicago Press, Chicago, 1996).
- [13] J. Memmott, N. D. Martinez and J. E. Cohen, *Predators, parasitoids and pathogens: species richness, trophic generality and body sizes in a natural food web*, J. Anim. Ecol. **69** (2001), 1–15.
- [14] T. W. Schoener, *Food webs from the small to the large*, Ecology **70** (1989), 1559–1589.
- [15] S. L. Pimm, J. H. Lawton and J. E. Cohen, *Food web patterns and their consequences*, Nature **350** (1991), 669–674.
- [16] S. J. Hall and D. G. Raffaelli, *Food webs: theory and reality*, Adv. Ecol. Res. **24** (1993), 187–239.

- [17] K. Havens, *Scale and structure in natural food webs*, Science **257** (1992), 1107–1109.
- [18] N. D. Martinez, *Constant connectance in community food webs*, Am. Nat. **139** (1992), 1208–1218.
- [19] N. D. Martinez, *Effect of scale on food web structure*, Science, **260** (1992), 242–243.
- [20] P. H. Warren, *Making connections in food webs*, Trends in Ecol. Evol. **9** (1994), 136–141.
- [21] P. A. Murtaugh and J. P. Kollath, *Variation of trophic fractions and connectance in food webs*, Ecology **78** (1997), 1382–1387.
- [22] L-F. Bersier, P. Dixon and G. Sugihara, *Scale-invariant or scale-dependent behavior of the link density property in food webs: A matter of sampling effort?* Am. Nat. **153** (1999), 676–682.
- [23] J. M. Montoya and R. V. Solé, *Topological properties of food webs: from real data to community assembly models*, (Santa Fe Institute working paper 01-11-069).
- [24] S. J. Hall and D. G. Raffaelli, *Food web patterns: lessons from a species rich web*, J. Anim. Ecol. **60** (1991), 823–841.
- [25] N. D. Martinez, *Effects of resolution on food web structure*, Oikos **66** (1993), 403–412.
- [26] G. Sugihara, K. Schoenly and A. Trombla, *Scale invariance in food-web properties*, Science **245** (1989), 48–52.
- [27] N. D. Martinez, *Scale-dependent constraints on food-web structure*, Am. Nat. **144** (1994), 935–953.
- [28] G. A. Polis, *Complex trophic interactions in deserts: an empirical critique of food-web theory*, Am. Nat. **138** (1991), 123–155.
- [29] N. D. Martinez and J. H. Lawton, *Scale and food-web structure — from local to global*, Oikos **73** (1995), 148–154.
- [30] K. O. Winemiller, *Spatial and temporal variation in tropical fish trophic networks*, Ecol. Monogr. **60** (1990), 331–367.
- [31] L. Goldwasser and J. Roughgarden, *Sampling effects and the estimation of food-web properties*, Ecology **78** (1997), 41–54.
- [32] J. E. Cohen *et al*, *Improving food webs*, Ecology **74** (1993), 252–258.
- [33] J. H. Lawton, *Webbing and WIWACS*, Oikos **72** (1995), 305–306.

- [34] N. D. Martinez, B. A. Hawkins, H. A. Dawah and B. P. Feifarek, *Effects of sampling effort on characterization of food-web structure*, Ecology **80** (1999), 1044–1055.
- [35] C. S. Elton, *Animal ecology*, (Sidgwick and Jackson, London, 1927).
- [36] G. E. Hutchinson, *Homage to Santa Rosalia or why are there so many kinds of animals?* Am. Nat. **93** (1959), 145–159.
- [37] L. Goldwasser and J. Roughgarden, *Construction and analysis of a large Caribbean food web*, Ecology **74** (1993), 1216–1233.
- [38] P. Erdős and A. Rényi, *On the evolution of random graphs*, reprinted in J. Spencer (ed) *The art of counting: selected writings*, (MIT Press, Cambridge, 1973).
- [39] J. E. Cohen, *Food webs and niche space*, (Princeton University Press, Princeton, NJ, 1978).
- [40] J. E. Cohen and C. M. Newman, *A stochastic theory of community food webs. I Models and aggregated data*, Proc. R. Soc. Lond. B **224** (1985), 421–448.
- [41] J. E. Cohen, *A stochastic theory of community food webs. VI Heterogeneous alternatives to the cascade model*, Theor. Pop. Biol. **37** (1990), 55–90.
- [42] A. R. Solow and A. R. Beet, *On lumping species in food webs*, Ecology **79** (1998), 2013–2018.
- [43] R. J. Williams and N. D. Martinez, *Simple rules yield complex food webs*, Nature **404** (2000), 180–183.
- [44] J. Maynard Smith, *Models in ecology*, (CUP, Cambridge, 1974).
- [45] E. C. Pielou, *Mathematical ecology*, (Wiley, New York, 1977).
- [46] J. Roughgarden, *Theory of population genetics and evolutionary ecology: an introduction*, (MacMillan, New York, 1979).
- [47] M. L. Rosenzweig and R. H. MacArthur, *Graphical representation and stability conditions of predator-prey interactions*, Am. Nat. **97** (1963), 209–223.
- [48] M. L. Rosenzweig, *Why the prey curve has a hump*, Am. Nat. **103** (1969), 81–87.
- [49] C. S. Holling, *The functional response of predators to prey density and its role in mimicry and population regulation*, Mem. Ent. Soc. Can. **45** (1965), 1–60.
- [50] M. P. Hassell, *The dynamics of arthropod predator-prey systems*, (Princeton University Press, Princeton, 1978).

- [51] J. Beddington, *Mutual interference between parasites or predators and its effect on searching efficiency*, J. Anim. Ecol. **51** (1975), 597–624.
- [52] R. Arditi and L. R. Ginzburg, *Coupling in predator-prey dynamics: ratio-dependence*, J. Theor. Biol. **139** (1989), 311–326.
- [53] I. Hanski, *The functional response of predators: worries about scale*, Trends Ecol. Evol. **6** (1991), 141–142.
- [54] R. Arditi, L. R. Ginzburg and N. Perrin, *Scale-invariance is a reasonable approximation in predation models — reply*, Oikos, **65** (1992), 336–337.
- [55] P. A. Abrams, *The fallacies of ratio-dependent predation*, Ecology **75** (1994), 1842–1850.
- [56] H. R. Akçakaya, R. Arditi and L. R. Ginzburg, *Ratio-dependent predation — an abstraction that works*, Ecology **76** (1995), 995–1004.
- [57] A. A. Berryman, A. P. Gutierrez and R. Arditi, *Credible, parsimonious and useful predator-prey models — a reply*, Ecology **76** (1995), 1980–1985.
- [58] G. Huisman and R. J. De Boer, *A formal derivation of the Beddington functional response*, J. Theor. Biol. **185** (1997), 389–400.
- [59] P. A. Abrams and L. R. Ginzburg, *The nature of predation: prey dependent, ratio-dependent or neither?* Trends Ecol. Evol. **15** (2000), 337–341.
- [60] A. Hastings and T. Powell, *Chaos in a three-species food chain*, Ecology **72** (1991), 896–903.
- [61] D. M. Post, M. E. Conners and D. S. Goldberg, *Prey preference by a top predator and the stability of linked food chains*, Ecology **81** (2000), 8–14.
- [62] W. M. Getz, *Population dynamics: a per capita resource approach*, J. Theor. Biol. **108** (1984), 623–643.
- [63] W. M. Getz, *A unified approach to multispecies modeling* Nat. Res. Mod. **5** (1991), 393–421.
- [64] A. A. Berryman, J. Michalski, A. P. Gutierrez and R. Arditi, *Logistic theory of food web dynamics*, Ecology **76** (1995), 336–343.
- [65] R. Arditi and J. Michalski, *Nonlinear food web models and their responses to increased basal productivity*, in *Food webs: Integration of patterns and dynamics*, (G. A. Polis and K. O. Winemiller, eds), pp. 122–133 (Chapman and Hall, New York, 1996).

- [66] B. Drossel, P. G. Higgs and A. J. McKane, *The influence of predator-prey population dynamics on the long-term evolution of food web structure*, J. Theor. Biol. **208** (2001), 91–107.
- [67] P. Yodzis, *Introduction to theoretical ecology*, (Harpers and Row, New York, 1989).
- [68] H. M. Hastings, *The May-Wigner stability theorem*, J. Theor. Biol. **97** (1982), 155–166.
- [69] J. E. Cohen and C. M. Newman, *When will a large complex system be stable?* J. Theor. Biol. **113** (1985), 153–156.
- [70] P. Érdi and J. Tóth, *What is and what is not stated in the May-Wigner theorem?* J. Theor. Biol. **145** (1990), 137–140.
- [71] D. L. De Angelis, *Stability and connectance in food web models*, Ecology **56** (1975), 238–243.
- [72] L. R. Lawlor, *A comment on randomly constructed model ecosystems*, Am. Nat. **112** (1978), 445–447.
- [73] P. Yodzis, *The stability of real ecosystems*, Nature **289** (1981), 674–676.
- [74] A. Roberts and K. Tregonning, *The robustness of natural systems*, Nature **288** (1981), 265–266.
- [75] P. J. Taylor, *The construction and turnover of complex community models having generalized Lotka-Volterra dynamics*, J. Theor. Biol. **135** (1988), 569–588.
- [76] S. L. Pimm and J. H. Lawton, *On feeding on more than one trophic level*, Nature **275** (1978), 542–544.
- [77] J. D. Pelletier, *Are large complex ecosystems more unstable? A theoretical reassessment with predator switching*, Math. Biosci. **163** (2000), 91–96.
- [78] K. McCann, A. Hastings and G. R. Huxel, *Weak trophic interaction and the balance of nature*, Nature **395** (1998), 794–798.
- [79] G. A. Polis, *Stability is woven by complex webs*, Nature **395** (1998), 744–745.
- [80] A. R. Ives, J. L. Klug, and K. Gross, *Stability and species richness in complex communities*, Ecology Letters **3** (2000), 399–411.
- [81] M. Loreau, *Biodiversity and ecosystem functioning: recent theoretical advances*, Oikos **91** (2000), 3–17.

- [82] S. L. Pimm, *Complexity and stability: another look at MacArthur's original hypothesis*, *Oikos* **33** (1979), 351–357.
- [83] S. L. Pimm, *Food web design and the effect of species deletion*, *Oikos* **35** (1980), 139–149.
- [84] C. Borrvall, B. Ebenman and T. Jonsson, *Biodiversity lessens the risk of cascading extinction in model food webs*, *Ecology Letters* **3** (2000), 131–136.
- [85] S. L. Pimm, *The complexity and stability of ecosystems*, *Nature* **307** (1984), 321–326.
- [86] W. Jansen, *A permanence theorem for replicator and Lotka-Volterra systems*, *J. Math. Biol.* **25** (1987), 411–422.
- [87] R. Law and J. C. Blackford, *Self-assembling food webs: A global viewpoint of coexistence of species in Lotka-Volterra communities*, *Ecology* **73** (1992), 567–578.
- [88] K. S. McCann, *The diversity-stability debate*, *Nature* **405** (2000), 228–233.
- [89] D. M. Raup, *Biological extinction in earth history*, *Science* **231** (1986), 1528–1533.
- [90] P. Bak, and K. Sneppen, *Punctuated equilibrium and criticality in a simple model of evolution*, *Phys. Rev. Lett.* **71** (1993), 4083–4086.
- [91] R. V. Solé and S. C. Manrubia, *Extinction and self-organized criticality in a model of large-scale evolution*, *Phys. Rev.* **E54**, (1996) R42–45.
- [92] F. Slanina and M. Kotrla, *Extremal dynamics model evolving networks*, *Phys. Rev. Lett.* **83** (1999), 5587–5590.
- [93] L. A. N. Amaral and M. Meyer, *Environmental changes, co-extinction, and patterns in the fossil record*, *Phys. Rev. Lett.* **82** (1999), 652–655.
- [94] M. E. J. Newman and R. G. Palmer, *Models of Extinction. A Review.* (adap-org/9908002).
- [95] B. Drossel, *Biological evolution and statistical physics*, *Adv. Phys.* **50** (2001) 209–295.
- [96] B. Drossel, *Extinction events and species lifetimes in a simple ecological model*, *Phys. Rev. Lett.* **81** (1998), 5011–5014.
- [97] J. Camacho and R. V. Solé, *Extinctions and taxonomy in a trophic model of coevolution*, *Phys. Rev.* **E62** (2000), 1119–1123.
- [98] P. Yodzis, *The structure of assembled communities. II.* *J. Theor. Biol.* **107** (1984), 115–126.

- [99] W. M. Post and S. L. Pimm, *Community assembly and food web stability*, Math. Biosci. **64** (1983), 169–192.
- [100] J. A. Drake, *Models of community assembly and the structure of ecological landscapes*, in *Mathematical ecology* (T. Hallam, L. Gross and S. Levin, eds), pp. 584–604, (World Scientific, Singapore, 1988).
- [101] J. A. Drake, *The mechanics of community assembly and succession*, J. Theor. Biol. **147** (1990), 213–233.
- [102] R. D. Morton, R. Law, S. L. Pimm and J. A. Drake, *On models for assembling ecological communities*, Oikos **75** (1996), 493–499.
- [103] R. Law and R. D. Morton, *Permanence and the assembly of ecological communities*, Ecology **77** (1996), 762–775.
- [104] R. D. Morton and R. Law, *Regional species pools and the assembly of local ecological communities*, J. Theor. Biol. **187** (1997), 321–331.
- [105] J. L. Lockwood, R. D. Powell, P. Nott and S. L. Pimm, *Assembling ecological communities in time and space*, Oikos **80** (1997), 549–553.
- [106] L. R. Belyea and J. Lancaster, *Assembly rules within a contingent ecology*, Oikos **86** (1999), 402–416.
- [107] G. Caldarelli, P. G. Higgs and A. J. McKane, *Modelling coevolution in multispecies communities*, J. Theor. Biol. **193** (1998), 345–358.
- [108] C. Quince, P. G. Higgs and A. J. McKane, *Food web structure and the evolution of ecological communities*, in *Biological Evolution and Statistical Physics* (M. Lässig and A. Valleriani, eds), (Springer-Verlag, Berlin, 2002).
- [109] C. Quince, P. G. Higgs and A. J. McKane, *The effects of the removal and addition of species on ecosystem stability*, in *Complexity emerging: a paradigm for ecological thought* (J. A. Drake, C. R. Zimmermann, S. Gavrillets and T. Fukami, eds), (Columbia University Press, New York), to be published.
- [110] M. Lässig, U. Bastolla, S. C. Manrubia, and A. Valleriani, *Shape of ecological networks*, Phys. Rev. Lett. **86** (2001), 4418–4421.
- [111] U. Bastolla, M. Lässig, S. C. Manrubia, and A. Valleriani, *Dynamics and topology of species networks*, in *Biological Evolution and Statistical Physics* (M. Lässig and A. Valleriani, eds), (Springer-Verlag, Berlin, 2002).